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Breeding Activities, Especially Nest Building, of the Yellowtail (*Ostinops decumanus*) in Trinidad, West Indies[1,2]

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(Text-figures 1-4)

MOST AUTHORS AGREE that two families excel at building complex nests—the Icteridae of the New World and the Ploceidae (True Weavers) of the Old World. This paper reports nest building and some associated breeding activities of the Yellowtail, *Ostinops decumanus,* of the Icteridae, as observed during ten days in late January, 1960, at the New York Zoological Society's Department of Tropical Research field station at Simla, Arima Valley, Trinidad, W. I., and discusses relevant literature.

Since F. M. Chapman (1928) made a three-year study of the courtship and breeding activities of Wagler's Oropendola, *Zarhynchus wagleri,* on Barro Colorado Island, Panama Canal Zone, the most comprehensive reports on the flamboyant displays and the complex hanging nests of this group of the Icteridae are by Skutch (1954) on the Montezuma Oropendola, *Gymnostinops montezuma,* and the Yellow-rumped Cacique, *Cacicus cela;* by Tashian (1957) who studied the Yellowtail at Simla; and by Schäfer (1957) who studied *Ostinops decumanus* and *Psarocolius angustifrons* in detail. Although these papers do not include critical analyses of nest-building motions, they allow me to make comparisons of the nest-building techniques. (These papers are referred to below without citation).

The four species of oropendola—*angustifrons, decumanus, montezuma* and *wagleri*—appear to be very closely related, and as a systematist trained in a field other than ornithology, I would not hesitate to include them in the same genus. However, the currently accepted generic names are used here. Table 1 lists outstanding features of the behavior during courtship and nest building shared by members of this group. Nest building suggests that they are close to the caciques—just how close may be revealed in further studies.

HABITAT

The Yellowtail nests in large numbers in the erythrina trees, *Erythrina micropteryx,* also called "bois immortel," introduced into the Arima Valley to provide shade in the cocoa and coffee plantations (Text-fig. 1). Although the cocoa, *Theobroma cacao,* coffee, *Coffea arabica,* and banana, *Musa paradisica,* trees planted under the erythrina are also introduced, all are readily accepted by the native birds. The undergrowth of most of Trinidad is cleared several times a year with long knives, locally called cutlasses. The cutting suppresses the heavy secondary growth that would compete with the local crops. Rising above the understory to an average height of 50 to 150 feet are the erythrina, whose orange-red blossoms cover their crowns early in the year at the close of the rainy season. Schäfer describes identical habitat for Yellowtails in Venezuela.

The ends of the erythrina branches are ideally suited for the attachment of the Yellowtail's nest, because (Text-figs. 3, 4) of the whorls of stiff, dead leaf- or flower-bases that extend two to five inches along the branch at the bases of the smaller branches. The bases of the nests we saw were woven into these burr-like structures. Furthermore, the trees are tall, with smooth bark, and at the top they spread umbrella-like

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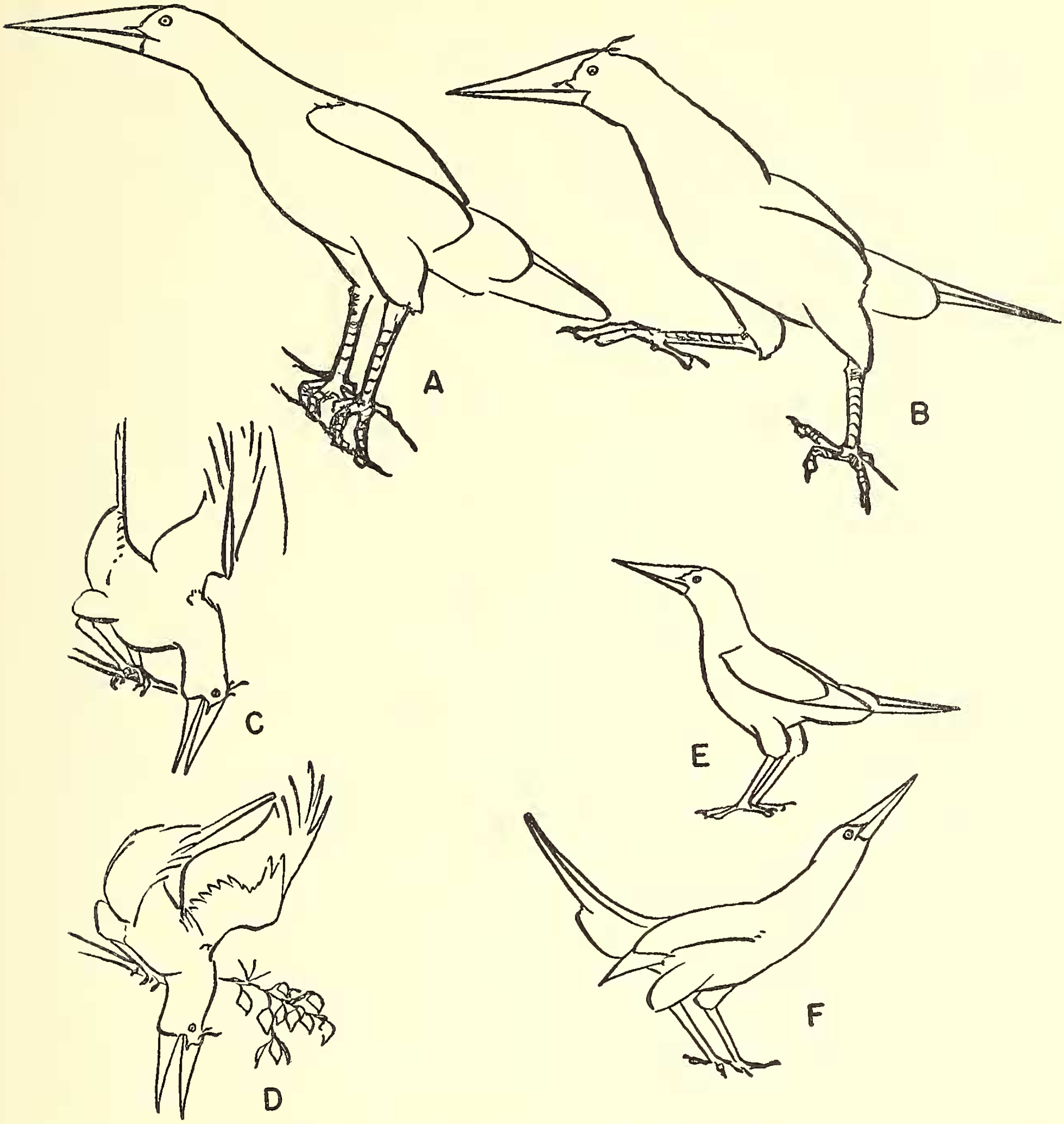
TEXT-FIG. 1. Part of Yellowtail nest colony in *Erythrina* tree. Nests 1 and 18 were studied during site establishment; nests 9, 10, 18 and 19 were studied during building of the sleeve, closing the entrance, and weaving the bag; nests 13, 15 and 19 were studied during weaving the bag and closing the bottom.

crowns which do not interfinger with each other. As Skutch points out, these characteristics provide sites that protect the nests from predators (chiefly lizards and snakes). He describes the destruction of a colony of Yellow-rumped Caciques to which a snake found access by vines growing up the trunk. Schäfer comments on the form of branch-tip preferred for nest establishment and the umbrella shape of trees chosen by *decumanus*, comparing them with the requirements of the forest-opening species, *angustifrons*, which places its nest on the wall of vegetation along roadsides.

TERRITORIAL BEHAVIOR OF THE MALES

Erythrina trees are scattered 40 to 50 yards



TEXT-FIG. 2. Display postures of Yellowtails. **A.** Anxious, subordinate male. **B.** Dominant male approaching intruder. **C.** Low level song posture given when alone, primarily territorial. **D.** High level song posture given when near a female, primarily sexual. **E.** Anxious and aggressive female in squabble near her nest. **F.** Soliciting female.

apart on the steep hillsides of the Arima Valley. Each dominant male Yellowtail appeared to occupy a territory covering two or three adjacent trees. The males in the colonies which Chapman and Skutch studied did not seem to have a territory or a set relation to any particular group of females. I agree with them that as soon as one male made a supplanting attack on another, the attacked bird left, suggesting dominance and territory defense, but I saw no territorial fights, nor did Schäfer. Schäfer's detailed discussion of territory in *decumanus* and *angustifrons* shows site tenacity and hierarchical arrangement among dominant and subordinate males around a colony tree. There are differences of degree, but in both species subordinate males intrude almost undisturbed, especially at the period of copulation.

When an "intruding" male came into a tree (even the nesting tree itself), he often spent as much as ten minutes there without being attacked. If the resident male did pay attention to the newcomer, however, he moved into the tree or branch, flying directly at the intruder or perching 20 yards away, then walking or hopping toward him with neck swollen and head point up slightly (Text-fig. 2B). Soon the intruder (Text-fig. 2A) left and shortly afterward both males sang. If, however, an intruding male bowed and sang, he was often rushed by the territory owner. In one instance the intruder left soon after the owner bowed and called twice.

The male has half a dozen song or patrol perches at which he spends most of his time. When active, he spends four to ten minutes at each perch. When inactive, he may be difficult to find—either he is away from his tree or sitting quietly on one perch. Schäfer has notes on the schedule of activities of territorial males and females.

I heard some sing all day, and the most active singing between 0600 and 0900, and between 1600 and 1930, local time, as did Schäfer. Tashian recorded the frequency of singing and reported no peaks, but that may have been because his study was made earlier in the reproductive season.

Song and Display.—The song is described in detail by Tashian, who used moving picture film to analyze and time the postures which accompany it. Schäfer separates territorial from nuptial song. As a bird starts his nuptial song, he drops his head steeply between his feet and raises his tail over his back, stiffly fanning his under tail coverts which, like his tail, are yellow. The bird then usually gives two hollow, gurgling calls and, standing in a deep bow with the feathers of his neck stiffly raised, gives a rattling trill (*eeeeoooo-eeeeoooo*, or *eedy-eedy-ooo*), which grades into a continued rustling made by flapping his relaxed but raised wings (Text-fig. 2D); then he stands up. He may repeat this call as often as every twenty seconds for two hours, but usually the call is relatively infrequent, given about once every three or four minutes. Schäfer reports every three minutes, or 10-20 times an hour, averaging 100 times a day. I found this call most frequently directed toward a single female or group of females. Schäfer found the noisy flight between perches so regular a prelude to this song as to be a part of it. He found that this call was less frequently given than the territorial song, and I agree.

The territorial call starts with (1) a rattling gurgle, or (2) a hoarse *tsteeee* or *tsreee-kleee*, ending in a series of "plop"-like calls—*ka-wow-wow-wow*. I did not see the posture which accompanied it and heard no wing-rustling with it. Usually it is given by an isolated male and, I believe, not necessarily in the presence of females. Schäfer says that the cry is given with raised and weakly beating wings, and with plumage not fully displayed (Text-fig. 2C).

The singing bird, especially away from a nesting tree, may alternate his song with feeding in the blossoms of the erythrina tree, but usually when he is singing he spends the time between songs moving among his trees, standing, peering around in the tree, preening wings, flanks and neck, ruffling feathers, scratching, pecking at his feet(between the toes) or wiping his bill. When in a nesting tree, the male occasionally flies vigorously (his wings make a deep resonant sound) to perch on the side of a nest that is completed or is being built. He lands with head already down and neck swollen, and gives his full song, perches stiffly, with crest raised, neck swollen and blue eye glaring, for ten or fifteen seconds, and then flies, usually to perch on the branch at the base of this same nest. I saw a male fly at and replace a female who had just flown in and landed on the nest, and several times a male responded to the arrival of a female or a group of females with a bow and a song. The male was especially likely to respond with song to the arrival of females if he had recently driven away another male.

Most of the time, even when the male flies to her nest, the female pays no overt heed to his activity. Occasionally she is evidently interested and watches him, usually with her head up and feathers sleeked (head-up "threat" of icterids, with some "fleeing tendency," Text-fig. 2E). I found no direct relation between song display and copulation. Schäfer does not suggest any close relation and points out that during the copulation period territoriality seems to be minimal.

During the day, males are usually isolated on territories, although many (young and inferior males, Schäfer suggests) visit other males' territories or nesting trees. In the evening males stay isolated in the crowns of the erythrina trees until after the evening roosting flights of females, which take place between about 1800 and 1830. Then males leave their territories and fly singly to the communal roosts which, in the Arima Valley, are in a large clump of bamboo at the bottom of the valley below Simla. On their roosting flights, females in groups of three to thirty come from several miles, usually in short flights between crowns of erythrinas. They stop in the territories of actively singing males and often engage in precopulatory actions. Males are the last to settle in the bamboo roosts. They start to sing on their trees again before the sun is up.

The females of any one nesting tree readily visit territories of other males, and I saw copulation less often in nesting trees than in other trees where a male was on station but where there were no nests.

Territorial Behavior of the Females

I counted 1, 3, 5, 22 and 43 nests in five different trees, each in a singing male's territory (Text-fig. 1). Females usually in groups of a dozen, but at times several dozen, fed in the cocoa and citrus trees and moved along the ridges down into the groves to gather nesting material and food. Actively building females spent much of the day working at their nests, while groups of females not especially attached to the nesting tree visited it for several periods of twenty minutes to half an hour.

As Skutch and Chapman report for their oropendolas, a number of Yellowtail females operated as a group and placed their nests on the same branch or on a series of branches close together. These nests were consistently placed on the leeward side of the tree and on the outer and upper part of the crown, at least 40 feet above the ground. Schäfer agrees, and has many details on choice of colony trees, location of nests, calendar and schedule of events which led up to colony establishment. He stresses the importance of weather changes which start the cycle, but does not mention subgroups of females within a colony.

When close together in what appears to be a squabble over the nest site, the females stand with heads raised to a 45° angle and with tail partly raised (Text-fig. 2F). I saw no fighting such as recorded by Skutch and Chapman, but frequently heard a nasal hiss, *garreeoo* or *aaah,* from birds in this circumstance. It resembled part of the song of a Starling, *Sturnus vulgaris.* The females crowded their nests together even within the limits of the group and four of the nests I watched being built were woven into a neighbor's or a previous year's nest. Schäfer mentions hostility of females to males and their fierce attacks on inept immature males that trespass at their nests.

Progress of the Breeding Cycle

Chapman, Skutch, Beebe (in Tashian) and Tashian agree that nest building starts at the very end of December and in early January. This coincides with the end of the rainy season. Chapman believed that for Wagler's Oropendola the start of the nesting season is more accurately associated with date than with the last of the rains, but Schäfer shows in detail how the downpours that come with cold, northerly winds start the cycle in *decumanus* and how humidity controls the start in *angustifrons.* Chapman reported the beginning of the breeding cycle as being signalled first by the arrival of individual males in the colony tree. Both Chapman and Skutch say that the real start is the arrival of groups of females to inspect the branches of the colony tree. Schäfer shows clearly that in *angustifrons* the males' territorial activity is a critical stimulus for the start of the nesting activity by females. If he stops his display, they stop.

Copulation.—The male Yellowtail sings in his tree, occasionally flies noisily and perches with a group of females who are preening or moving among the branches. The females may ignore him or may move away nervously, with their heads slightly raised and feathers sleeked (Text-fig. 2E). This activity continues through the early stages of nest building. Schäfer shows that copulation receptivity appears in females of both *decumanus* and *angustifrons* as they finish the nest bag and line it.

When receptive, the female flies to a branch near a male. Twice I saw a female fly to a male from inside her nest, and on other occasions females came "out of the blue" into an isolated song tree. The female perches above or near the male with feathers sleeked, head raised and tail raised or horizontal, and may almost imperceptibly flutter her wings. The male, with neck swollen, hops and walks along the branches to perch below and beside her. The female squats and flutters her wings, with head and tail slightly raised; the male mounts for about ten seconds while both birds flutter their wings. The male dismounts and, in my observations, flies rapidly away at once. On landing, he wipes his bill and continues his patrolling and singing. After ruffling and shaking her feathers, the female usually either started to preen or flew off. Schäfer's notes are very brief but agree with these. Tashian reports that the male sang and displayed and pecked at the female's cloaca before copulation, and that he displayed again after copulation. I have notes on several sequences in which a male approached a female as in copulation and then pecked violently at her cloaca, but these preliminaries did not lead to copulation and suggest rejection by the female.

Asynchronous Activities of Groups of Females.—All authors agree that many females start nests much later in the season than the main group. Chapman felt that some may have been second nests. Schäfer emphasizes the place of immaturity. In one of Chapman's groups of late-nesting females, building was interrupted and then the beginning of the rainy season caused them to abandon the colony site. Skutch found a colony in northern Honduras feeding nestlings in September. As with so many birds, the breeding cycle of the oropendolas must be started by a regular annual time-giver, and breeding continue until interrupted by some internal or environmental time-giver—in this case, the next rainy season.

There is also variation in the timing of an individual female's breeding during the species peak in late January. At the tree I watched, there were about a dozen females prospecting, four nests being started, six nests being built, about thirty idle nests or with females incubating, and at least five nests with females feeding young. Females regularly came and perched near the idle nests and clucked, or they flew in and perched head down in the entrance for twenty seconds, turned and perched looking out for thirty seconds to a minute, then flew off.

Nest Building

Building Material.—(See Table 1 for details of nest-building materials used by the five species. Schäfer describes them in detail for *angustifrons* and *decumanus*).

Schäfer says that *decumanus* collects materials among the trees and off the ground, at a distance from the colony, while *angustifrons* collects material low in undergrowth or on the ground under the colony. Skutch describes the collecting of fibers underneath a banana frond by a female *montezuma,* and the actions are similar to those used by (1) the Baya, *Ploceus philippinus,* in India when nipping and tearing strips from the base toward the tip of a rice leaf, *Oriza sativa,* (Ali, 1931); and (2) by the Village Weaver, *Textor cucullatus,* tearing leaves of Elephant Grass, *Pennisetum purpureum,* (Collias, 1959).

My observations showed that *decumanus* uses chiefly long, fibrous strips and grass. The materials are green when brought to the nest, but turn brown in a day or two. In many cases the fruiting heads of the grass (resembling *Panicum*) were still visible. On other occasions small vines with tiny green leaves (resembling the *Solanum* family) were used. Schäfer says that the supports and weave are chiefly (80%) liana tips, and that the packing between is entirely Spanish moss, *Tillandsia usneoides* if available. He describes the material used by *decumanus* as slender and fine, in contrast to the characteristically coarse and turgid material available in the forest interior and used by *angustifrons.*

Skutch describes *montezuma* folding over the strips from the banana frond in order to carry long pieces. Yellowtails brought their material in unfolded or gathered into loops in the bill, and often the material streamed far out behind the bird as she flew (Text-fig. 1).

When the female Yellowtail starts to build, she uses pieces that average 30 to 45 cm. long; then, as she finishes the base and builds the supports at the entrance, she brings fewer pieces per trip and they are 60 to 100 cm. long. She brings many shorter pieces again as she weaves the sides. When weaving the bottom, she brings a few long pieces (100 to 150 cm.). These appear to be strips of banana leaf.

Skutch speaks of violent squabbles over nest-building materials in *montezuma* and no squabbles in the Yellow-rumped Cacique. Schäfer describes frequent violent fights in *angustifrons* and few in *decumanus.* Chapman describes the stealing of loose ends from slovenly nests or from those of absent birds by *wagleri,* as does Skutch in *montezuma.* These two species may demolish a messy nest. Schäfer comments that stealing is usual in *angustifrons,* infrequent in *decumanus.* I saw very little grabbing of material from other nests. On one occasion a female repeatedly flew past a nest with a moplike mass hanging below the finished entrance, and each time she grabbed a hanging, loose end and tried to fly off with it, usually unsuccessfully. On another occasion, a female perched several minutes on the outside of a nearly completed nest, pecked and seemed to try to pull out the tiny, still-green fibers sticking out or looped through the brown weave. Another time a female perched on the outside of the nest and repeatedly pushed her bill through the weave, opening it and making a series of fairly large holes, but not pulling anything out. In each case the visitor left when the builder came back, but in no case did the builder chase her. Schäfer says that young males make holes in the sides of nests during the period when females are receptive.

Schäfer discusses nest building in *decumanus* and *angustifrons,* emphasizing differences in location, placing of the nest, and the materials used. His data are very largely on *angustifrons,* and although he describes the phases of building (anchoring the nest and weaving; building the apron; building the ring and the future entrance; building the bag; and bringing the nest lining), he does not treat in detail the movements involved.

Phase 1: Site Establishment.—When the female is establishing her nest site, she spends from five to fifteen minutes perched at a fork in a branch at the tips of the long branches of the erythrina (Text-fig. 3A and B). She walks and hops, alternating her feet, along the main part—peering, looking under and over the forks near the tip. She spends much time peering out across the valley. Skutch and Chapman describe frequent squabbles in groups of females inspecting branches. Schäfer describes threat postures, but no real fights. I found the females inspecting alone, and saw no squabbles among the few birds prospecting. There were several squabbles among the females on lower branches where nests were already established.

When the female first brought material (long grass or vines), she perched and looked around, moved, looked around, flew to another branch, stepped on the grass and gathered another loop, then flew to another part of the tree. At two sites, where females had been prospecting on previous days, I watched a female bring long grass in her bill and, perching on the branch, look, move, look, then push it into the dead leaf petiole bases at the joint (Text-fig. 4D). These females brought several loads before the grass remained in place. The female may or may not step on the grass with one foot (Text-fig. 3C); she may grasp an end in her bill, gather another loop, pick up all the material, and fly off again; she may do no more, and just fly off; or she may take bits of the grass and push them down into the clump of dead leaf bases, then reach around the branch and pull a strand up around the branch (Text-figs. 3E & 4A); or she may pull a loose end around a leaf base and poke it into the mass of material with a short shake (four or five times) of her bill—the tremble-shove (Lorenz, 1955). When building the base of the nest, the female pulls ends *around* and uses the bill-shake more conspicuously than when weaving the sides of the nest.

I found the females hesitant and irregular in their activity when establishing the nest site, but I think this may have been caused by my presence. Schäfer suggests that activity during this period is readily interrupted.

Phase 2: Establishment of the Nest Base.—The female brings grass and may put her foot on the newly-brought material (Text-fig. 3C), or may merely push it into the tangle already in the leaf base. Soon after some material hangs down, she pushes the new material into the mop (apron, *tablier*) just under the branch. When the mop is short, she usually pulls only a little and just "fiddles" with loose ends, then flies off. As the mop lengthens, she tucks the new material under the branch and, reaching over to the other side, grasps a piece of grass in the very tip of her bill (Text-fig. 3D), often with a little shake as she takes it. She pulls this gently or firmly toward her and tucks it into the grass on her side of the branch, with two or three pokes and four or five shakes of her bill. Or she takes a piece of grass from the side nearest her, pulls it over and tucks it into the grass around and behind the branch, with the same bill-shakes. Usually she worked two, three or four times from her side of the branch, then shifted to reach behind and work from there. She often worked for several minutes without touching the green grass which she had just brought. I did not establish that she worked with the same piece of grass, but the fact that she did no alternate pecking on one side and tucking into the other with the reverse, suggests that she was not working with a particular blade.

The only action I saw during the building of the base was "peck-pull around-tuck"—with the grass held in the leaf base or under the female's feet. She put her foot on the nesting material only during the first day or two (as Schäfer also reports), but worked on the base for twice that length of time. As more grass was added, the female pulled harder at the loose and long ends of the grass.

Comment.—My notes show consistent differences in the construction of the nest base by the Yellowtail, when compared to the other oropendolas and cacique. According to Chapman and Skutch, *wagleri* and *montezuma* weave the pliant material around and around the branch, and they suggest that the bird wraps an individual piece and ties it to the branch before working with a new piece. Schäfer's notes agree more closely with mine, but in *angustifrons* he suggests that when the female brings in the first long fibers, she does give each one individual attention in wrapping them around the branch, and further, that she may perch and swing on the hanging end as if testing its security.

Phase 3: Transition to the Sides of the Nest.—Soon there is a loose mop of fibers about 10 cm. long hanging from the fork of the branch and extending 7 to 10 cm. along both sides of the fork, and then the female shifts to the next phase of building. Now, instead of perching with both feet on the branch (Text-figs. 3C, D, E & 4A), she perches with one foot on the branch and the other on the mop which is hanging from the branch (Text-fig. 4B). Her weight on the hanging fibers causes the apron to elongate. The female still pokes the grass into the woven material near the branch, but now pokes it only into the mop and not on top of the branch. She still consistently pulls the grass around something (either the branch or the edge of the material hanging from the base) and uses the peck-pull around-tuck movement. Thus she weaves over the branch and also binds or "overcasts" the edge of the material on the two "open" sides of the nest's horseshoe-shaped base (Text-fig. 3F).

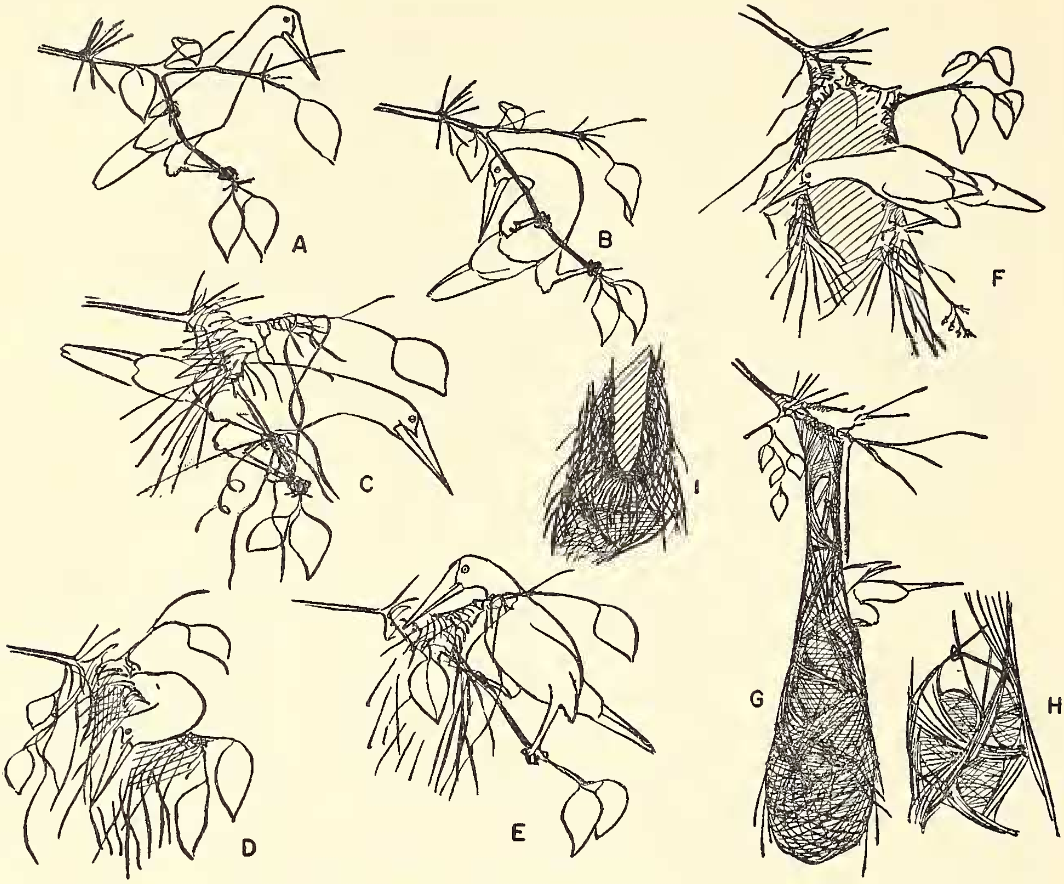
Table 1. Comparisons of Behavior in Courtship and Nest Building

Character	*Gymnostinops montezuma*	*Zarhynchus wagleri*	*Ostinops decumanus*	*Psarocolius angustifrons*	*Cacicus cela*
Roosts	Bamboo		Bamboo	Palms	
Male's call		chuck	chac	quic	
Alarm	cack	chack-chack	kak-kak-kak	chak-chak	
Male's alarm panics colony	p	p	p	a	
Male's song	*tsu ta ta ooo tsreee kleee a wow wow wow*	Deep, liquid, "hope you choke," sputtering cackle, crash	Melodious *tschuudu du du du tshuuii wup wup wup*	Bell-like melody 3-6, soft thick crescendo to explosive 5-6	Brilliant and varied
Territory	Several males, 1 tree	Several males, 1 tree	Several males, several trees. 1 male dominant and subordinate males present	Several males, several trees. 1 male dominant and 2-3 subordinates.	Several males, 1 tree
Territorial song			*eedy eedy ooo cherie du du du wup wup wup*	Melodious and shorter than song, emphasis on 2 & 3	
Song bow	p	p	p	pa	
Raises on toes	p	p	p	pa	p
Neck swollen		p	p	pa	p
Eyes glare		Blue	Blue	Green-brown	
Tail up during song		p Flicked	p	½	p
Wing-waving during song	p	a	p	pa	p
Male flight noisy	p	p	p	pa	
Enlarged bill	p	p	p	p	p
Presence of crest	p Small	p	p	p small	
Courtship away from colony	p	p	p	a	p
Dark central tail feathers	p	p	p	p	
Females outnumber males	Several times	6 to 1	p	p	p
At least polygamous	p	p	p	p	p
Sex size-difference	p	p	p	p	p
Territorial fights	a	a	a	a	a
Female preens male's neck		p	a	p	
Male pecks female's cloaca			(a) p	a	p
Females associate in flocks	p	p	p	pa	p
Female threat	*raah* whine	*raaah* whine	*tcherie garreeoo* or	Hiss *raah*	
Female alone builds	p	p	p	p	p
One tree	p	p	p	a	
Nest at end of rain	p	p	p	a	p
Short-distance migrant	a	p	p	a	
Female territory		p	p	p	
Height of nests	15-35 m.	> 35 m.	10-20-35 m.	5-8 m.	> 15 m.
Roof over entry	a	a	a	a	p
Female chooses site			p	p	
Terminal hanging branch			p	p	
Isolated tree	p	p	p	a	p

TABLE 1. COMPARSIONS OF BEHAVIOR IN COURTSHIP AND NEST BUILDING *(continued)*

Character	*Gymnostinops montezuma*	*Zarhynchus wagleri*	*Ostinops decumanus*	*Psarocolius angustifrons*	*Cacicus cela*
Nests close together	p	p	p	5-10 over 100-200 m.	p
Leeward side of tree	p	p	p	a	
Base in whorl of leaf bases			p	p	
Previous year's base		p	p	p	
Materials			Slender & fine	Coarse & turgid	
Palm strips and fibers	p		p	p	p
Tendrils—vines	p	20-25 cm. long	80% at start		p
Bark strips		p	p		
Air roots			p		
Weed stalks	p	p			
Grass and sedge			p	p	
Bromeliads			Nearly all of interstices		
Lining					
Leaves	Dead & dying p	Soft leaves, fibers	Dry p	Green {Bromeliad, Sedge, Heliconia}	Kapok cotton
Bark		p			
Collect			At distance	Near nest	
Steal loose ends	p Often	p Often	Rarely	p Often	
Nest Building					
Base of wrapped tendrils	p (knots)	p	p	p	p
Head over limb, reaches under to grasp	p	p	p	p	
Apron	p	p	p	p	
Convert to loop	p	p	p By uniting edges	p By uniting edges	p
Standing in ring	p	p	a	a	p
Work head down	p	p	(p) a	a	p
Enter by door		p	p May enter below	p May enter below	
Enters on wing—no pause	p	p	a Only if hurried	a	
Perches and pauses as leaves	p	p	p	p	
Female works inside	p	p	p	p	p
Building time	14-16	23-25	9-25	19-33 ad. 17-51 yg.	
Nest length	60-120 cm.	55-100 cm.	125-137 cm.	76-140 cm.	30-45 cm.
Large diameter	17-23 cm.	20 cm.	20-22 cm.	20-22 cm.	
Incubation days	@ 14	17	17-19	19-20	
Nestling days	@ 30	36	28-34 or 31-36	25-30	

p = action or article is present.
a = action or article is absent.
pa = action or article may be present or absent.
Blank means no observation is available.



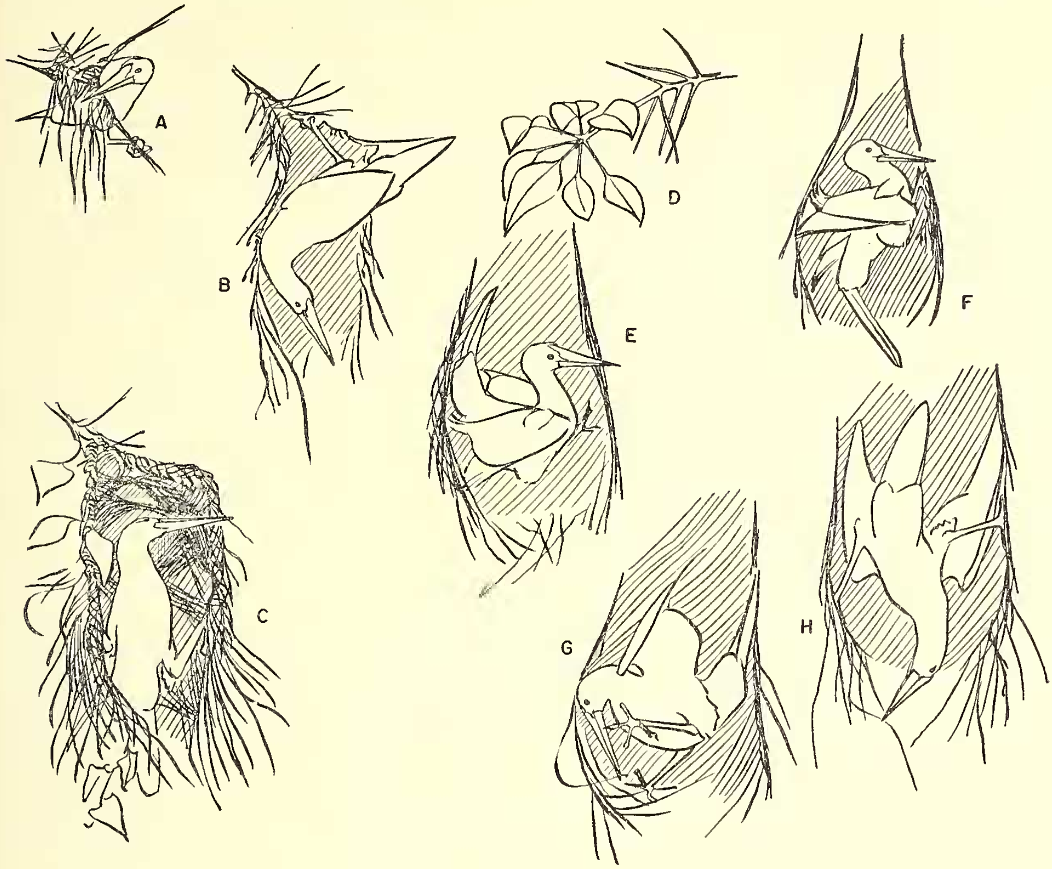
TEXT-FIG. 3. Nest-prospecting and nest-building postures. **A. & B.** Investigating possible nest site, Phase 1, at Nest 1. (Note cluster of previous year's leaf bases). **C.** Looking over valley before leaving, Phase 2, when nest base is still a ball-like snarl at the fork. **D. & E.** Reaching over and down for a loose end to pull up over and tuck, Phase 2. **F.** Perched on the hanging apron, reaching across to pull around and tuck—the first stages of closing the entrance, Phases 4 and 5. **G.** Pattern of grasses in Nest 5, with female perched in entrance feeding young. **H.** Detail of pattern of weave in the side of a nest. **I.** Detail of the weave at the base of the entrance—Nest 9.

At first (at least one day) she perches as often with both feet on the branch as with one foot down, but as the material gradually lengthens she spends more time perched on the hanging material. Later she may again perch with one foot on the branch, even after the two halves are partially joined together (see below).

Phase 4: Buldiing the Sides of the Entrance.—Now, as the female returns with fibrous material, she perches with both feet on the hanging, tangled mop. She works between her feet with her head up, pokes her load of grass into the woven material, reaches out and around, pecks, pulls out and up, brings head in, and pokes with three or four shakes of her bill; or she pecks, pulls out and around behind, and pokes in behind with a shake.

At this stage she adds a new motion: she first stuffs the large beakful of rather short material into her work; then she pushes her bill through the material, grasps a bit in the tip of her bill, pulls it back toward her, then moves it horizontally and pokes it into the weave again—with or without a short (four or five) shake. I refer to this as "horizontal peck-pull-poke." Schäfer considers this action specific to the wadding or filling (*bourrage intercalaire*).

As long as she weaves with both the peck-pull around-tuck and the horizontal peck-pull-poke, she weaves the supporting structure—the horseshoe-shaped cross-section—with overcast edges. This part of the nest often has holes in it because the bird spends most of her time overcasting the edges. She spends less time working with



TEXT-FIG. 4. Nest-building postures. **A.** Working on the nest base, Phase 2 at Nest 1. **B.** Working on the apron, Phase 3 at Nest 9, when still perching on the branch. **C.** Perched on the two halves of the apron, Phase 5 at Nest 10, starting to work the edges together. **D.** Branch tip of *Erythrina,* showing this year's cluster of leaves and last year's shriveled leaf bases. **E. & F.** Perched inside nest, working on the nest bag below the entrance hole, Phase 6 at Nests 13 and 19. **G. & H.** Reaching below feet to pull hanging pieces in closing the bottom of the nest, Phase 7 at Nests 13, 15, 19.

the horizontal peck-pull-poke which weaves the fabric of the bag. The supports of the nest are thus straplike, tied together tightly by connectors, but they do not form an evenly woven bag (Text-fig. 3H); crudely, they resemble the braided handles of a string shopping bag. Schäfer says that *decumanus* usually works head-down (in contrast to my observations), but that *angustifrons* works on the apron head-up.

Phase 5: Closing the Base of the Entrance.—(Schäfer calls this the ring and future entrance). To start joining the two sides below the entrance, the female uses the horizontal peck-pull-poke on the material which hangs loose and frayed across the open bottom of the horseshoe-shaped sleeve, and, as Schäfer says, she uses long pieces at this stage. At first she perches on one side and takes a bit of grass from the same side, pulling it across to poke it into the other (Text-fig. 3F). Finally, she perches with one foot on each side of the horseshoe, and works strips across from one side into the woven part on the other (Text-fig. 4C). She may work either on the outside or the inside of the sleeve, and may spend all of several visits below the entrance, working horizontally on the lower part of the structure. This transition may be seen as a gradual increase in use of the horizontal peck-pull-poke, until it is applied all around the bag and replaces the peck-pull around-tuck. She closes the gap, still using a combination of the horizontal weaving and overcasting actions, but her attempt to join the sides is not immediately successful; usually she starts to bring the two sides together about a foot above the place where they are ultimately joined. The entrance may be 30 to 45 cm. long if she starts to close it soon after the apron is large enough for her to perch on, or it may be 60 to 90 cm. long if she continues to weave with the overcasting action. This accounts for differences in lengths of the hanging nests. Nests vary from just over two to more than four feet long (60 to 120 cm.). Schäfer emphasized that the difference in experience between young and old females may explain the observed differences in length.

When the base of the entrance is closed and the apron has become a sleeve, the female spends a long time working with the overcasting motion on the margin at the base of the entrance. At this point the pull-around is vertical. Thus she weaves a buttonhole-like stitch along the bottom of the entrance (Text-fig. 3I). Her weight, coming and going, pulls the material down, and by pulling it thus makes the dense weaving stronger where she perches to enter. Before the entrance is well sewed in, she usually still hitches up woodpecker-like to the branch to perch and look around before she flies off. Entrances are on the lee side of the nest.

Phase 6: Building the Sides of the Nest.—While she is working on the sides and supports of the nest, the female characteristically works on the inside, but often works on the outside. As soon as the bottom of the entrance is firmly closed, she does almost all her work on the inside. As far as I could see, she uses chiefly the horizontal peck-pull-poke action and brings larger beakfuls of material (on an average 30 to 60 cm. long).

As the female works inside the bag, she sits woodpecker-like (her tail may be bent up behind her in the the sleeve and occasionally her wings may be partly opened (Text-fig. 4E & F). She works four or five minutes, reaching slowly and carefully through the weave to grab a bit of fibrous material in the tip of her bill, pull it toward her, then poke it through again, often with a little shake. There is less pulling, tugging and wrapping of long pieces, and more delicate attention to detailed weaving. Also, she spends much less time, proportionately, gathering building materials at this stage.

Now she starts to add a new movement. After about every ten to fifteen horizontal weaving actions, she reaches down between her feet to peck, pull up and poke (Text-fig. 4G & H). The longer she continues to use only horizontal weaving, the longer the bag of the nest.

Where two nests are built immediately next to each other, the female may carry her weaving action across into the material of the adjacent nest, as Skutch pointed out. I observed this in the case of nests #7 and #13 (Text-fig. 1). Skutch described how one bird, building thus into a neighbor's nest, seemed to make its own nest an additional length below the bottom of the neighbor's nest so that there was a "proper" length of bag hanging down. The two females I watched did the same. This suggests that a definite length of bag stimulates the bird to the next activity, which leads to closing the bottom. Crook's (1960) discussion of the change of stimuli which leads to changes in the building techniques used by weaver finches agrees with this.

Phase 7: Closing the Bottom.—During the building of the sides, the female perches with both feet at the same level, above or just below her bill, and works reaching ahead, beside or between her feet. In closing the bottom, she reaches way down between her feet, almost doing a somersault (Text-fig. 4G and H), grasps the long, hanging strands, pulls them up to eye-level, and weaves them into the side—pulling and poking with little or no evident shaking of her bill. As she moves around she gradually takes more and more bits from one side and weaves them into the opposite side. This closes the bottom. But because of her weight and her inefficient actions, she is not immediately successful. The stage at which she shifts to closing the bottom and her success with the cross-weaving govern the length of the hanging bag. She continues to weave horizontally, alternating work on the sides and on the bottom. Schäfer reports that young female *angustifrons* may have to try several bottoms before they succeed.

Chapman, Skutch and Schäfer commented that their birds entered the nest only through the entrance—once the entrance is formed. While building the sides, the Yellowtail usually enters and leaves by the entrance, but may often fly in and out through the bottom of the nest, even after she has started to close the bottom.

When the first strands are hooked across the bottom, the female spends much time weaving between her feet, pulling especially hard on the grass with which she is working. During this action her wings are often partly raised and her tail is pushed hard against the side of the bag (Text-fig. 4G). Her pushing movements inside and her weight as she climbs up the sides combine to enlarge the gourd-like bottom, and to pull the strands taut. Schäfer comments on the joggling and pushing inside the nest during this phase, which forms the 25 cm. diameter of the bag.

Phase 8: Lining the Nest.—My observations at one nest suggest, as do Tashian's, that the birds use bits of leaves, chiefly erythrina, to line the nests. I could not see the motions used in forming this lining because the nest screens them. Movements visible on the outside of the bag, however, showed that the bird frequently changed her position, joggling the nest, and that her wings and tail were raised. Other birds, whose nest-molding activity has been recorded in detail, thrust the breast forward by pushing the feet back and up, and Schäfer's observations show that *decumanus* tramples the nest-lining materials (torn fragments of dried, brown leaves) while turning around and around.

This is the period of the female's receptivity to copulation.

Attentiveness to Building.—The birds build fitfully as they weave the base and may be absent for several days. Schäfer says the period lasts one to nine days, according to the level of stimulation and to the female's age. As the sides of the nest are started, they still build sporadically and may be absent for a day or two, but then work with energetic spurts of concentrated activity. Schäfer says the closing of the ring takes one to six days and that an inexperienced *angustifrons* worked 16 days and built down 1 m. before successfully closing the entrance. After the birds start to weave the hanging sleeve, they work constantly until the bottom of the nest is partly closed, which takes four to five days (Schäfer). Then they may be absent for a day or two before the bottom is brought together. Once finally started on the bottom, they work constantly until it is closed, but they may pause again before weaving the thick bottom and lining the bag which takes two to six days. Even when the heavily woven bottom is finished, the female may spend hours slowly and carefully weaving horizontally part way up the bag.

Discussion

Function of the Territory.—Skutch and Chapman commented on the peculiar territory structure in the oropendolas. They were unable to establish whether a male took up a territory and defended it, and whether pairing was promiscuous or polygamous. Schäfer compares territorial behavior in *decumanus* and *angustifrons* in detail but does not comment.

Males seem to give their attention temporarily to one group of females and readily shift attention to a new group. In the Yellowtail, my observations point to isolation of males on their own defended territories, but although I watched for 35 hours at one tree with 43 nests (long enough to expect to observe frequent copulations if they were restricted to the male whose territory included the nesting tree), I saw copulation there only twice. During the same period I saw eight copulations in trees with no nests. This suggests either (a) that the females are nesting in one particular male's territory but each is paired to a specific male whose territory may be elsewhere, or (b) that the females nest together in one male's tree by flock formation among the females without regard to sexual relations with any particular male. There may be polygamy, no pair formation or "standard" pair formation. The restriction of the term "pair formation" to those cases in which copulation takes place only with the pair partner, may not necessarily apply to these birds. Such limitations gratuitously suggest some form of propriety—which may be anthropomorphic. My notes, and Schäfer's, show a hierarchy of several males associated with a colony tree. Thus there is territory but its exclusiveness is modified. Schäfer points out the lowering of territorial "jealously" during the copulation period in *decumanus* and what appears to be complete promiscuity in both species where inferior males intrude to copulate with receptive females while the dominant male is occupied.

Chapman and Skutch suggest that groups of females establish a new nesting site and that the presence or absence of the male is unimportant; in fact, the males seem to follow groups of females. Schäfer's observations, especially of *angustifrons*, show the necessity of the territorial males' constant stimulation to arouse and carry through the females' interest in nesting.

These observations and mine lend support to Tinbergen's (1957) explanation of the function of territory; namely, the combination of a need for the male to act in a specific way recognizable by females and other males during pair formation, coupled with a need for the male to have a fixed location. The site, in the case of the oropendolas studied by Skutch and Chapman, seems to be a group of females rather than a map area. With this change in structure, it may become selectively advantageous to the species to de-emphasize the aggressive aspects of the display of the male or lower his tendency to exclude other males. Thus, the male goes through his song display to stimulate the female, but he is not necessarily bound to drive away other males, and the female does not necessarily restrict her attentions to one male or the male in whose territory she builds. I can see no way in which food enters directly into the selective advantage of territory in this case.

Closing the Ring.—The building of the entrance by the Yellowtail contrasts with that described by Skutch and Chapman for their species. Their birds weave an apron across the fork and then, standing on the material, push an entrance through the partly woven material which then becomes a circle or loop. This loop is used as a perch, and the sleeve is woven downward from it—the bird hanging head down into the sleeve. Although they do not dwell on details, the descriptions of these authors suggest that their species use techniques of building the base and loop which are similar to those used by the True Weavers (Ploceidae) as reported by many authors (Friedmann, 1922, Ali, 1931; Grzimek, 1952; Collias, 1959; and Crook, 1960).

The techniques which Schäfer and I describe are similar, and differ from those of the weavers. While the weavers make a ring first and build the nest bag out from the ring, which becomes the mouth of the bag, *decumanus* and *angustifrons* build a hanging apron (horseshoe-shaped in cross-section) directly down from the foundation on the branches and join the free ends to form the ring and the entrance. The techniques of weavers and oropendolas resemble each other in the weaving of free-hanging ends from one side into the other, but differ in the location of the ring in forming the nest foundation, and (at least in *decumanus*) differ also in that the female oropendola works with her head at the level of her feet or above, while the male weaver works with his head down below his feet.

Skutch watched one *montezuma* after her properly formed circle was broken when her neighbor stole some loose ends. The robbed female perched with one foot on each side of the ring and in this "uncomfortable" position closed the two sides in the same way as I observed the Yellowtail to do. This suggests that the two systems may not be fundamentally different in the oropendolas.

Entering and Leaving.—Both Skutch and Chapman observed that the returning bird darts swiftly into the nest entrance as soon as it has been formed. They suggest that the fast disappearance into the bag and the long look around before leaving serve to avoid predation. In building the foundation and sides of the nest, however, the female Yellowtail perches on the outside and is conspicuously exposed. Even so, she peers around over the valley just before flying away. Also, later in the cycle, when she visits the completed nest or comes to feed the young, she perches for ten to twenty seconds with her head down inside the bag and her yellow tail hanging out conspicuously. This action must deny the significance of the fast dart into the entrance as only to avoid predation. There may be advantage to the peering around before leaving, but it would seem that the technique of entering may be dictated as well by the bird's heavy wing-loading which exposes her to the danger of stalling as she flies up sharply to the entrance.

Techniques of Nest Building.—Herrick (1911) pointed out that the stereotyped movements used by birds to build their nests are convenient tools for the comparative study of behavior and its evolutionary aspects, yet little work has been done since. Later, Laven (1940a) repeated this suggestion. Several authors have described the nest-building activities of birds that nest on open ground, especially the non-passerine species, *e.g.*, Selous (1902) and Brock (1911) for the Lapwing, *Vanellus vanellus;* Portielje (1925) for the Cormorant, *Phalacrocorax carbo,* and (1928) for the Herring Gull, *Larus argentatus;* and Tinbergen (1931) for the Common Tern, *Sterna hirundo,* and (1936) for the Herring Gull. Several studies have shown how universal certain nest-building actions are. Although the loons, *Gavia stellata,* (Huxley, 1923) and grebes (Huxley, 1914; Selous, 1901) merely drop their nesting weeds, moss or mud on the nest edge, most birds add them with some form of tremble-shove: Cormorant (Portielje, 1925, and Kortlandt, 1940); herons (Lorenz, 1955); storks (Schüz, 1943); and perching birds, Raven, *Corvus corax* (Lorenz, 1940). Friedmann's (1922) study of the building actions of the Ploceidae was one of the very few on perching birds until the Second World War. In 1943, Nice mentioned the appearance of generalized nest-building actions in the developing behavior of young Song Sparrows, *Melospiza melodia,* and since then several authors have reported on the early appearance of these fundamental actions (Dilger, 1956; Goodwin, 1954; Kramer, 1950; Nicholai, 1956; and Schüz, 1943).

Nest-building actions, more or less modified, are used by many species as part of courtship actions, *e.g.*, Great Crested Grebe, Cormorant, herons, woodpeckers, Lapwing and other shorebirds, Alcidae and estrildid and ploceid finches. In addition, certain of the actions associated with nest building, and thus presumably primarily sexual, have been transferred to aggressive action, *e.g.*, scraping by Ringed Plover, *Charadrius hiaticula,* (Laven, 1940), and Killdeer, *Charadrius vociferus;* nestling and scraping by Collared Flycatcher, *Ficedula albicollis,* (Löhrl, 1951; Curio, 1960); and grass pulling by Herring Gulls (Tinbergen, 1951 and 1952). Moynihan (1955) argues, however, that grass pulling by Herring Gulls is not transferred from sexual motivation, but is directly aggressive as redirected attack.

Kluijver (1949/1955) seems to have started the revival of detailed studies of nest-building techniques. He describes the building actions of the Great Reed Warbler, *Acrocephalus arundinaceus;* van Dobben (1949) describes the building actions of the Icterine Warbler, *Hippolias icterina* and Chaffinch, *Fringilla coelebs;* and Kramer (1950) describes the nest-building actions of the Red-backed Shrike, *Lanius collurio.*

Kluijver, van Dobben and Kramer define the fundamental actions of nest building in passerine birds as three: (1) nestling—the bird presses its breast down into the nest-cup, usually with bill and tail pointed upward; (2) trampling—the bird presses its breast to the bottom of the nest-cup and kicks vigorously and repeatedly with each leg, backward and upward (3) pecking, tugging and tucking—the bird reaches forward and grasps nest material, pulls it one way or the other, and tucks it into the nest again. These actions are the same as Herrick (1911) describes for the nest building of the American Robin, *Turdus migratorius,* Red-eyed Vireo, *Vireo olivaceus,* and Baltimore Oriole, *Icterus galbula.* Additional detailed studies of a number of passerine species show how widely distributed these actions are: Sylviidae—Lesser Whitethroat, *Sylvia curruca,* and Blackcap, *Sylvia atricapilla,* Dechert (1955), Icterine Warbler, van Dobben (1949); and Great Reed Warbler, Kluijver (1949/1955); Paridae—Long-tailed Tit, *Aegithalos caudatus,* Maxse (1951), Tinbergen (1953b), and Bearded Tit, *Panurus biarmicus,* Koenig (1952); Sittidae—European Nuthatch, *Sitta europaea,* Löhrl (1958); Ploceidae—Baya, Ali (1931), and Village Weaver, Grzimek (1952), and other weavers, Crook (1960); Estrildidae of several species, Kunkel (1959); Turdidae—European Blackbird, *Turdus merula,* E. and I. Messmer (1956); Muscicapidae, Löhrl (1951), Curio (1960); Fringillidae—Chaffinch, van Dobben (1949), Marler (1956); and Emberizidae—Song Sparrow, Nice (1943).

All these studies show that the movements used by passerine birds in placing nest material and forming the nest-cup are uniform and widespread, but as Dechert (1955) illustrated, the important thing is the sequence of these actions, the materials used and how they are used. Her study of the Lesser Whitethroat and Blackcap showed that these closely related species used nearly identical actions but different materials, and that they used the actions in different proportions, thus creating quite different nests. A further illustration of the importance of the material chosen is given by Lorenz (personal communication) who, when first keeping some Red-billed Weaverbirds, *Quelea quelea,* discovered that they were unable to build their huge nests because the grass native to Germany did not "stick." He obtained some of the grass the birds use in their native Africa and found that the leaves of this grass are "retrorsely scabrous" on their margins (have small tooth-like spines on their edges), causing the leaves to cling together. Ali (1931) realized the importance of the scabrous margins of rice leaves in the nest building of the Baya. Schäfer's study also shows the importance of different nesting materials in similar species, but his study also shows use of different actions (in anchoring the base). Nickell, (1958) examined nesting materials and nest types of 169 species of eastern North American species.

In a number of families scattered among the perching birds, some of the generalized actions have atrophied and some actions have been added to the basic repertory. The estrildid finches (Kunkel, 1959) built their messy, domed nests with the following actions: (1) the bird, standing in the middle of its nest, grabs material with its bill and pushes it away, or it may simply push at the wall and roof of the nest with its head; (2) the bird grasps material and pulls sideways, either to the left or to the right; (3) the bird pulls material directly toward itself into the cup. In these actions, the birds have lost certain of the basic behavior sequences and their nests seem to reflect this.

It is interesting, in terms of the former classification of the estrildid finches with the ploceid finches (Steiner, 1955), that they share two unusual nest-building actions: (1) termination (Crook, 1960)—a grass stalk held in the beak is moved by a rotating motion of the bill until it is held at one end; (2) to stretch the building material and form the pocket-like nest, the builder pushes against the walls with its head or bill.

The highest development in nest building, nearly all authors agree, occurs in two families—the Old World True Weaver Finches (Ploceidae) and the New World blackbirds, troupials and orioles (Icteridae). Ploceids such as the Red-billed Weaverbird studied by Friedmann (1922), the Baya described by Ali (1931), the Village Weaver described by Grzimek (1952) and studied and photographed by Collias (1959), and the species discussed by Crook (1960), use additional actions to weave and tie knots in their material in order to fasten it to the foundation branches. According to Friedmann (1922) and Crook (1960), the True Weavers take a fiber in the bill, hold it at the end, place it on a branch (sometimes holding it with the foot), then take one end of the fiber and push it to the far side of the branch. Reaching around the other side, they take the strand and tuck it under the part they are standing on, then pull taut the knot that has been made. The fiber is repeatedly drawn round and round, each time being inserted within the previous loop. The end may also be looped in and out through the already-woven fabric.

Collias (1959) describes "four basic mechanisms in working a grass strip into its nest. He tends (1) to bend the strip about some object, either a twig, another grass strip, or his own leg; (2) to double a strip back on itself; (3) to alternate the direction in which he winds the strip about objects such as twigs or other grass strips; and (4) to poke and pull a strip through holes, normally the interstices of the nest materials. It is in the possession of mechanisms (3) and (4) that a true weaver (Subfamily Ploceinae) differs from other weaverbirds. . . The end of a strip is often looped back on itself in such a way that pulling on the strip tightens its attachments. This is essentially a hitch type of knot. Knots of other types than the hitch are rare." In this specific treatment of an individual fiber, the action of these birds differs from that of many Icteridae. They tuck a bill full of fibers into the nest material and then may ignore them until dealt with again "by accident."

In the ploceid finches, the foundation of the nest is made by forming a loop on which the bird stands and which it uses as an entrance from which to build the sleeve that will become the nest bag. The caciques and oropendolas studied by Skutch and Chapman resemble the True Weaver Finches in building a similar loop. These authors also suggest that the birds wind the strands around the branches to form the foundation of the nest. However, my study of the Yellowtail, and Schäfer's, show that such behavior is not characteristic of *decumanus* and *angustifrons.*

The New World orioles have specific actions peculiar to themselves which are slight modifications of the generalized ones of most perching birds: pecking, pulling around and tucking (Herrick, 1911, Baltimore Oriole). Herrick showed that after the nest bag was constructed, the Baltimore Oriole also used the standard trampling, nest-molding technique. The fact that the enormous and complex nest of the Yellowtail is built by simple actions which are used by other species to make much simpler nests, points to the generalization that variation is built out of specializations of a few fundamental "inventions."

To emphasize this, Selous (1902) and later Kramer (1950) pointed out that the scraping actions of plovers and sandpipers, gulls and terns, are homologous with the trampling actions of perching birds making their cup-shaped nests. Similar trampling actions are found among a number of the Laro-limicolae: Lapwing, Selous (1902), Brock (1911), Rinkel (1940) and Laven (1941); Turnstone, *Arenaria interpres,* Bergman (1946); Northern (Red - necked) Phalarope, *Phalaropus lobatus,* Tinbergen (1935); Common Tern, Tinbergen (1931); Caspian Tern, *Hydroprogne caspia* or *tschegrava,* Bergman (1953); and Herring Gull, Tinbergen (1936). Furthermore, these studies show that there are other nest-building actions in gulls and terns (and my own studies show that the same is true in sandpipers, *Calidris bairdii,* and plovers, *Charadrius vociferus* and *Ch. melodus,* similar to those of perching birds. When sitting on its scrape, the bird picks up material and either drops it over the shoulder or pulls it immediately in front of itself and drops it. These actions are identical to the sideways pulling or the peck-pull around-tuck action of perching birds. The big difference, of course, is in the choice of nest-building material, the uniformity of treatment and concentration given to the material. Shorebirds and gulls either use no material, cast the material aside, or do not pursue the treatment to a final resting place.

Many small perching birds may spend two or three days building; the Red-eyed Vireo spends approximately five. The Yellowtail may spend three to five weeks. A Killdeer may spend two to three weeks scraping, and then continue for another three weeks throwing nest material over its shoulder, or pecking, pulling and dropping material on the edge of the nest after the eggs have been laid until they hatch. The bird usually kicks with its feet five to ten times in the trampling movements each time it settles on the nest. In the Piping Plover the persistence of this action is functional. It is used to uncover eggs that have been buried by blowing sand. Similar actions are used to uncover buried eggs by the Kentish Plover, *Charadrius alexandrinus,* and the Little Ringed Plover, *Charadrius dubius,* (Walters, 1956), and by Kittlitz's Sandplover, *Charadrius pecuarius,* (Hall, 1958), which regularly covers its eggs when frightened from them.

Clearly, the type of action and the amount of time spent on the action does not control the end product. But there seems, in fact, to be a sequence in the intensity of attention paid to the nesting material from (a) the very careless handling by shorebirds and gulls through (b) the sloppy work of the estrildid finches, to (c) the situation found in most perching birds, and finally (d) to the True Weavers and icterids. In the evolution of nest building (which is at least in part independent of the evolution of those factors used in classification), similar motions have been applied to different types of material, and a change has been made according to differences in the "plan in mind" and perseverance to that plan: specialized actions added, and new reactions appearing to specific building situations. The difference is not in the motion (the tool) but in the central nervous system, which in turn is modified, within limits, by changes in environment which influence the living bird (see especially the differences in the nest building of young and old female *angustifrons* studied by Schäfer).

Stereotyped Behavior and Brain Structure.—In considering the modification of behavior patterns in evolution and according to experience of the individual organism, the basic difference in brain structure between birds and mammals must be taken into account, as described by Cobb (1960). In birds, the basal area of the forebrain, the *corpus striatum,* has been greatly enlarged. This is the area associated with quick, complex physical co-ordination. In contrast, the roof of the forebrain in mammals has been developed—an area whose specialization has tended toward associations developed during the experience of the individual.

The impression of bird behavior is of stereotyped responses (consistent and efficient) that are uniform as they occur, but whose occurrence is modifiable between species and according to experience of the individual bird. Certain stimuli or events change the bird's instructions and its behavior shifts. When watching the Yellowtail construct its nest—operating steadily and mechanically with a smooth, weaving action for a period of time, and then shifting over to a new system of weaving—I was strongly reminded of the control on an automatic loom by a card. The machine's motions—and the bird's—do not have the ability to change the card. The ability to change the card must, in a very crude way, be the organism's ability to learn and associate. The bird's actions are efficient in its present circumstances and, through evolution, suitable to its environment. During the bird's life, it seems that inherited material is as if carded and in units, and during maturation the bird "learns" what conditions, stimuli or parts of the environment are suitable for the expression of that inborn activity. The nest building of the Yellowtail is an illustration of the complex train of activity patterns that is changed to another complex train by a stimulus, rather than an illustration of a series of simple actions built up by association into complex trains, as seems to be the product of much mammalian learning.

But this illustration does not clarify the crux of the questions presented by the shifts in nest-building behavior by the Yellowtail. What combination of "things" leads to the decision to change the "card?" How does the bird treat inconsistent information upon which it must base its decision? For example, the behavior of a bird whose nest has been partly destroyed by the robbing of nest-building material by its neighbor. There must be a "look" (Thorpe, 1956; Crook, 1960; ? *Gestalt*) about the material and the state of construction which influences the sequence of activities that the bird follows. This hypothesis is supported by several natural tests resulting when several males work at the same nest (Crook, 1960). The bird's actions are neither guided exclusively as if by the unravelling of a string, as seem to be the activities of an insect, nor yet with the gradual brick-by-brick building of the association of learned actions into a whole, as may be the case with much mammalian development.

Summary

1. Yellowtails nest in colonies, 2-43 nests in the Arima Valley, chiefly in *Erythrina micropteryx,* an introduced shade tree towering over the cocoa, coffee and banana tree plantations.

2. A dominant male defends two or three neighboring trees but allows intrusion of subordinate males if the intruder does not display. Males have a territorial and a sexual song.

3. Males hold territories in nestless trees, and females copulate with males other than the dominant male of the colony tree.

4. Groups of females within a colony, nest according to a schedule independent of other groups.

5. Nest-building material is collected in valley bottoms away from the colony tree; it is chiefly grass, sedge and thin vines. The building material averages 30-45 cm. when the female starts the base, 60-100 cm. when building the supports and sides of the entrance, 30-45 cm. in weaving the bag, and 100-150 cm. when closing the bottom. The nest appears to be lined with dried leaves.

6. Detailed observations of nest-building technique show that a few simple movements are used and that the fibrous strips are dealt with by chance—not woven in individually. Actions are:

(a) Push billful of material into the work, reach over and grasp any end, pull around and tug, tuck in with tremble-shove. The female may perch on the branch or on the apron that she in making when using this technique;

(b) Push billful into the work, push bill through and grasp end, pull out and move to the side, tuck with a shake. The female perches woodpecker-like on the side on the nest;

(c) When closing the entrance, the female weaves across the two free edges, then overcasts the edges to bind the entrance with a buttonhole-like stitch;

(d) She uses chiefly the horizontal movements in making the bag, whose length seems to be measured by distance below the entrance. In closing the bottom, she reaches down between her feet to peck, pull up and poke.

7. The bird's attentiveness to nest building varies, being least at the start, strongest when building the sides of the nest, and interrupted before the bottom is closed and the nest lined.

8. Discussion:

(a) Territory in Yellowtails suggests purely courtship function. Copulation appears to be promiscuous;

(b) Closing the entrance and weaving the sides of the nest, as observed by Schäfer and myself, use different techniques than have been described so far;

(c) It is not clear why females hesitate on the nest entrance when entering and leaving;

(d) A review of nest-building techniques shows that three fundamental movements are widespread even among non-nest builders such as gulls and plovers. To these movements some groups have added actions by which they construct sloppy or elegant nests. The fine nests of the ploceid weaver finches are based on persistent individual attentions which tie knots in the fibers. Among the Icteridae, the fiber gets attention by accident, once it has been pushed into the work. Closeness of weave and security of attachment result from persistent repetition of actions.

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